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Stable isotopic and mesowear reconstructions of paleodiet and habitat of the Middle and Late Pleistocene mammals in south-western Germany.

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22 **Abstract**

23 Teeth are the most informative remains in the fossil record due to their abundance and enamel
24 structure, which is the hardest and most mineralised tissue, preserving well biochemical and
25 mechanical features. Teeth occlusal wear signal (mesowear) and stable carbon isotope composition
26 are reliable proxies for diet abrasiveness and habitat openness in ungulates, respectively. Both
27 methods are rarely compared in paleohabitat reconstructions. We examined the relationship
28 between stable isotopes and mesowear of large Pleistocene herbivores in south-western Germany
29 for the first time and reported unpublished stable isotope data from Villa Seckendorff. We found
30 significant differences in $\delta^{13}\text{C}$ among individuals, exhibiting sharp versus round cusps and high
31 versus low occlusal relief. The $\delta^{13}\text{C}$ and mesowear correlation was significantly positive among the
32 fossil assemblages but not among individuals because individuals varied in the amount of abrasive
33 dietary material. Species with the same mesowear were rather flexible in habitat and plant
34 communities' exploitation. The woolly rhinoceros *Coelodonta antiquitatis* had the highest
35 mesowear values, indicating abrasive grass-dominated diet, whereas *Bos primigenius* and *Bison*
36 *priscus* demonstrated the highest $\delta^{13}\text{C}$ values, indicating the most open environments. A negative
37 correlation trend was indicated between mesowear and $\delta^{18}\text{O}$ values and extrapolated temperature.
38 Sympatric species demonstrated different mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, suggesting diet or habitat
39 partitioning within a C3 plant ecosystem. Interestingly, temperate assemblages demonstrated more
40 variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, revealing ecological flexibility and diversity and generalist features
41 during the interglacial periods compared to glacial periods and boreal conditions.

42 **Keywords:** Pleistocene, Europe, stable isotopes, mesowear, paleoenvironment, temperature,
43 ungulates.

44 **1. Introduction**

45 Stable isotope biochemistry and wear signal of teeth enamel are the most exploitable methods,
46 exploring past environments and ecology of modern and fossil species. There are, however, only a
47 few studies, combining these methods in fossil environments (Tütken et al., 2013; Loffredo and
48 DeSantis, 2014). In our study, we combined a proxy for diet abrasiveness in herbivorous mammals
49 (mesowear) with a proxy for habitat openness (stable carbon isotopic ratios, $\delta^{13}\text{C}$) and a proxy for
50 temperature (stable oxygen isotopic ratios, $\delta^{18}\text{O}$), to demonstrate relationships among them in
51 temperate and boreal fossil environments.

52 We present new data on mesowear of the studied ungulates from Mauer, Steinheim an der Murr and
53 Villa Seckendorff localities as well as previously unpublished data on stable carbon and oxygen
54 isotope composition of large ungulates from Villa Seckendorff. The studied localities characterised
55 different climatic conditions during the middle and late Pleistocene (see also the section 2.1). Villa
56 Seckendorff represented glacial conditions during the earliest Weichselian glaciation (Koenigswald,
57 1985). Steinheim an der Murr, combined of several pits, corresponded to the glacial stage of MIS
58 10 and the Holsteinian interglacial MIS11 (Shreve and Bridgland, 2002). Steinheim's pit Sammet
59 species quite uniformly represented the most open and coldest habitat, whereas all other Steinheim
60 an der Murr pits Fritz, Baur, Sigrist, Gruber and Muller demonstrated more closed forested
61 environment with variations in obtained water and temperature, suggesting either more closed
62 canopy and humid (or aquatic) habitats as well as similarly colder and much warmer habitats than
63 Sammet (Pushkina et al., 2014). The oldest locality, Mauer sands, characterised interglacial
64 conditions of the early middle Pleistocene, correlated to MIS15 (Wagner et al., 2011).

65 We hypothesise that mesowear and stable carbon isotope values are positively correlated because
66 ungulates in open environments tend to feed on abrasive plants, such as grasses and sedges, which
67 are abundant in open types of landscapes. We expect mesowear to have a correlation with the stable
68 oxygen isotopic values and, thus, extrapolated temperature.

69 **1.1 Mesowear analysis**

70 Mesowear analysis examines a wear signal of worn occlusal surfaces and cusp shapes of
71 selenodont, ectolophodont or plagiolophodont ungulates' teeth, evaluating sharpness and relief.
72 Thus, it distinguishes between browsers that glean leaves, bark and green stems of dicotyledonous
73 plants from grazers that feed on grass and clip vegetation at or near ground level. Tooth wear can be
74 produced by attrition –dominated feeding (where most of the wear is caused by tooth rubbing on
75 tooth) or abrasion (tooth rubbing on abrasive food (e.g. grass)). The relief and sharpness of the worn
76 occlusal surface give a robust signal of the abrasiveness of the plant material eaten by the ungulates,
77 and has been shown to reflect the amount of grass in diet in particular (Kaiser et al., 2013; Kubo
78 and Yamada, 2014; Saarinen and Lister, 2016). Increasing abrasiveness results in lower and
79 increasingly rounded wear-induced morphology, and finally low relief and blunt cusps in highly
80 abrasion-dominated feeders (e.g., grazers) (Fortelius and Solounias, 2000). In general, browsers
81 feeding on softer foods have sharper and higher teeth cusps, whereas grazers feeding on more
82 abrasive material have lower occlusal relief and blunter teeth cusps.

83 **1.2 Carbon stable isotopes ($\delta^{13}\text{C}$)**

84 Carbon isotopic composition in mammalian enamel apatite reflects the presence of C3 and C4
85 vegetation in lower and mid-latitude habitats as well as a degree of canopy closure versus openness
86 in wooded high-latitude habitats (Vogel et al., 1978; Alcock, 1988). C3 plants, or woody
87 vegetation and grasses that have a cool growing season, have $\delta^{13}\text{C}$ values ranging between -34‰
88 and -23‰, with a suggested mean of -27‰ (Calvin and Benson, 1948; Hatch et al., 1967; Smith
89 and Epstein, 1971; Ehleringer and Monson, 1993; Kohn and Cerling, 2002). The canopy effect can
90 result in up to 5‰ differences in $\delta^{13}\text{C}$ in the same species at one site in pure C3 forest environments
91 between the herbivores feeding in a heavily enclosed wooded environment or on plants from
92 different tree elevation, and the herbivores feeding in more open parkland or grassland

93 environments with higher evapotranspiration (van der Merwe and Medina, 1991; Bocherens et al.,
94 1999; Feranec and MacFadden, 2006; Drucker et al., 2008; Hofman-Kaminska et al., 2018).

95 The $\delta^{13}\text{C}$ values of the carbonate fraction of bioapatite in large mammalian herbivores are higher
96 than or enriched by 14‰ compared to their diet: $\delta^{13}\text{C}_{\text{bioapatite}} = \delta^{13}\text{C}_{\text{diet}} + 14\text{‰}$ (Cerling and Harris,
97 1999; Cerling et al., 1999). In warm temperate and cold boreal environments $\delta^{13}\text{C}$ values higher
98 than -13‰ in herbivore enamel indicates open landscapes, such as grasslands and steppes, in which
99 the plants have $\delta^{13}\text{C}$ values higher than -27‰ in diet or ecosystem $\delta^{13}\text{C}$ values, ‰, whereas tooth
100 enamel $\delta^{13}\text{C}$ values lower than -13‰ indicate woodlands and denser forests (Bocherens, 2014).

101 **1.3 Oxygen stable isotopes ($\delta^{18}\text{O}$)**

102 Oxygen isotopic composition in enamel apatite reflects the source and amount of body-water, either
103 ingested from free drinking water or obtained from food and plants, thus, being a proxy for
104 variations in $\delta^{18}\text{O}$ values of meteoric water, which depend on the source of precipitation, affected
105 by latitude, altitude, continentality, temperature, evaporation and seasonality (Dansgaard, 1964;
106 Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995; Bryant et al., 1996; Kohn, 1996;
107 Sponheimer and Lee-Thorp, 1999; Levin et al., 2006). Crudely, the higher $\delta^{18}\text{O}$ values of meteoric
108 water correlate with warmer or dryer environments and vice versa (Dansgaard, 1964). Thus,
109 herbivores feeding in open steppe habitat are expected to have more enriched $\delta^{18}\text{O}$ values than the
110 species from forested cooler and more humid habitat. Obligate or water-dependent and evaporation
111 insensitive drinkers usually have $\delta^{18}\text{O}$ values lower than non-obligate or evaporation sensitive
112 drinkers, due to the consumption of evaporated water from plant leaves (Ayliffe et al., 1992; Bryant
113 and Froelich, 1995; Levin et al., 2006), being dependant on water availability and seasonality of
114 rainfall. Seasonal variation in rainwater in mid- and high latitude environments and species
115 migration can be significant, producing intra-tooth variations of 3-4‰ in hypsodont ungulates with
116 long enamel mineralization times, or more (e.g. in high-crowned ungulates, horses and bison,

117 Hoppe et al., 2004; Feranec et al., 2009). Oxygen isotopic composition can also be affected by life
118 history and physiology of mammals. Oxygen isotopic compositions are higher in nursing animals
119 during lactation and weaning periods because of milk consumption, which is related to the body
120 water in the mother, and more enriched in ^{18}O due to the preferential loss of ^{16}O through sweat,
121 urine, and expired water vapour (Bryant and Froelich, 1995; Kohn, 1996).

122 **2. Materials and methods**

123 **2.1 Regional setting and data**

124 We studied ungulate species from the Middle and Late Pleistocene localities in south-western
125 Germany (Table 1, Figure 1). We used two localities associated with temperate forested
126 environments: Mauer and Steinheim an der Murr, combined from the pits Sigrist, Fritz, Bauer,
127 Muller and Gruber, used as one locality assemblage (hereafter, in text Steinheim combined), and
128 two localities associated with glacial open habitat: Villa Seckendorff and Steinheim an der Murr pit
129 Sammet (hereafter, Steinheim Sammet). Their geological ages are corresponding to MIS 15 for
130 Mauer, MIS 11 for Steinheim combined, MIS 10 for Steinheim Sammet and MIS 5 a-d for Villa
131 Seckendorff. The stable carbon and oxygen isotopic composition of the species in Mauer and
132 Steinheim an der Murr pits, used in this article, were reported in Pushkina et al. (2014).

133 **2.2 Mesowear analysis**

134 For the mesowear scoring we used the methodology introduced by Fortelius and Solounias (2000),
135 where they analysed the worn occlusal surfaces of the second upper molars in selenodont,
136 ectolophodont or plagiolophodont ungulates by scoring the relief of the occlusal surface (cusp
137 height in relation to antero-posterior length of the occlusal surface) as high or low and the shape of
138 the cusps as sharp, rounded or blunt. The examples of mesowear scoring are shown in Figure 2.

139 We used predominantly the second upper molars in moderate wear stages, and in some cases the
140 first or third upper molars in order to increase the sample sizes. To analyse the dietary signals of the
141 ungulates among the localities, their mesowear scorings were transformed into numeric values on a
142 scale from 1 (low dietary abrasiveness, attrition-dominated tooth wear) to 3 (high dietary
143 abrasiveness, abrasion-dominated tooth wear), using the method from Saarinen et al. (2016):

- 144 1. The shape of the cusps was coded as a numeric value from 1 to 3 (1 = sharp, 2 = rounded, 3 =
145 blunt) and the height of the cusps as 1 or 3 (1 = high, 3 = low).
- 146 2. A “shape value” was calculated as the arithmetic mean of the shape values and a “height value”
147 as the arithmetic mean of the height values in the sample of teeth of a species from a locality.
- 148 3. The mesowear value for the population of a species from a locality was calculated as the
149 arithmetic mean of the “shape values” and the “height values” of a species from a locality.

150 This method of coding mesowear as a univariate value is similar in principle to that used by Rivals
151 et al. (2007) but instead of using numeric values from 0 to 3 for each combination of cusp height
152 and shape we use average values of cusp height and shape for calculating the total mesowear value.
153 The significance of this is that it does not assume tight correlations between cusp shape and relief.
154 Although blunt cusps typically occur in combination with low relief, all other combinations of cusp
155 shape and relief occur as well, with the most typical combinations being high and sharp, high and
156 rounded, low and rounded and low and blunt, reflecting increase in abrasion on the cusps. However,
157 sharp cusps do occasionally occur in combination with low relief, for example, in equids, reflecting
158 high-pressure chewing on very tough but not necessarily abrasive plant material (Fortelius and
159 Solounias, 2000).

160 **2.3 Isotope analyses and preparation of teeth enamel samples**

161 The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ratios were obtained from enamel carbonate fraction of the same teeth as for
162 mesowear scoring. Enamel samples were either mechanically separated and ground to a finer

condition in an agate mortar or drilled with a diamond-impregnated rotary tool. The uppermost surface of the tooth was removed before sampling usually by drilling with a dremel© borer. Samples of approximately 20 mg were analysed. Both fossil and modern samples of the enamel powders were pre-treated following the method described by Bocherens et al. (1996) but using the Continuous Flow (CF) for collecting carbon dioxide (Jacques et al., 2008; Bocherens et al., 2009). Our experience with fossil material from limestone cave has shown that the pretreatment used here is strong enough to remove exogenous carbonates but we are aware of possible slight changes of the oxygen isotopic composition of tooth enamel carbonate (Bocherens et al., 2009). Enamel powders for carbon and oxygen isotope analyses of structural carbonate within biogenic apatite were first reacted with 2.5% Sodium hypochlorite (NaOCl) for 24 h at 20° C to oxidise organic residues and rinsed with distilled water. This procedure was repeated twice. Then the remaining powder was treated with 0.1 M buffer acetic acid-calcium acetate (pH = 4.75) for 24 h at 20° C to remove exogenous carbonate (Bocherens et al., 1996; Koch et al., 1997; Ecker et al., 2013), and finally washed with distilled water and dried at 45° C. Then the treated powders were reacted with 100% phosphoric (= orthophosphoric) acid H₃PO₄ at 70° C for 5 hours to produce CO₂. The carbon and oxygen isotopic ratios were measured with a Finnigan Mat 252 mass spectrometer with an attached Gasbench II at the Geochemistry Laboratory, University of Tübingen. This system is particularly well suited for fossil enamel carbonate isotopic analysis because it has an integrated chromatographic column rather than a cold trap (Bocherens et al., 2009) and it allows for the analysis of the gas evolved from the reaction with orthophosphoric acid 10 times instead of one as with the Multiflow system from Micromass (Tütken et al., 2007). Therefore, it removes the contaminants better and produces purer CO₂ (Bocherens et al., 2009).

Stable isotopic results are expressed as the following standard δ -notation:

$\delta^E X = [(R \text{ sample}/R \text{ standard}) - 1] \times 1000$, where $^E X$ is $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$, and R is $^{13}\text{C}/^{12}\text{C}$ or $^{18}\text{O}/^{16}\text{O}$, respectively. The standards are the marine carbonate VPDB (Vienna PeeDee Belemnite) for carbon

188 and oxygen, and VSMOW (Vienna Standard Mean Ocean Water) for oxygen. The newly reported
 189 data from Villa Seckendorff samples were run in February 2011 and were the same as for the rest of
 190 the samples on Mauer and Steinheim, reported in Pushkina et al. 2014 (NBS18 ($\delta^{13}\text{C} = -5.00$, $\delta^{18}\text{O}$
 191 $= -22.96$ ‰, relative to VPDB); NBS19 ($\delta^{13}\text{C} = 1.95$, $\delta^{18}\text{O} = -2.20$ ‰, relative to VPDB)).

192 **2.4 Drinking water $\delta^{18}\text{O}$ value calculations**

193 We calculated temperature and drinking water values from oxygen isotope values, converting
 194 isotope composition of structural carbonate to its equivalent in phosphate with the use of three
 195 comparative equations that are robust for many different species:

Lecuyer et al., 2010	Iacumin et al., 1996	Zazzo et al., 2004
$\delta^{18}\text{O}_\text{C} = 1.035 \delta^{18}\text{O}_\text{P} + 8.33$	$\delta^{18}\text{O}_\text{C} = 1.02 \delta^{18}\text{O}_\text{P} + 8.67$	$\delta^{18}\text{O}_\text{C} = 1.03 \delta^{18}\text{O}_\text{P} + 8.35$

196
 197 Testing those 3 conversion formulas between oxygen isotope composition of structural carbonate
 198 and phosphate, we eventually obtained three temperature values for the sites. Iacumin's formula
 199 produced consistently lower values than Lecuyer's formula and Zazzo's consistently higher than
 200 Lecuyer's formula. Therefore, the comparisons and correlations of temperature values were done
 201 using the formula after Lecuyer et al. (2010).

202 The oxygen isotope composition of phosphate was converted to that of drinking water of different
 203 groups of species, according to equations below and reformulated based on original data from cited
 204 papers according to Skrzypek et al. (2011):

D'Angela & Longinelli, 1990 (deer)	Bernard et al., 2009 (bison)	Ayliffe et al., 1992 (elephant)	Sanchez et al., 1994 (horses)
$\delta^{18}\text{O}_\text{P} = 1.13 \times \delta^{18}\text{O}_\text{W} + 25.5$	$\delta^{18}\text{O}_\text{W} = 1.18(\pm 0.07) \times$ $\delta^{18}\text{O}_\text{P} - 27.2(\pm 1.1)$	$\delta^{18}\text{O}_\text{P} = 0.94(\pm 0.10) \times \delta^{18}\text{O}_\text{W} +$ $23.3 (\pm 0.7)$	$\delta^{18}\text{O}_\text{P} = 0.74(\pm 0.08) \times \delta^{18}\text{O}_\text{W} + 22.$ $0(\pm 0.6)$

205
 206 Based on current relationship between air and water (Skrzypek et al., 2011) we calculated
 207 temperature (°Celsius), using the formula: $T_{\text{air}} = 1.804 \delta^{18}\text{O}_\text{W} + 26.02$ for Central Europe (Krakow,
 208 Poland).

209 **2.4 Comparison of mesowear and stable isotope ratios**

210 To compare mesowear with stable carbon and oxygen isotope signals and temperature within
211 ungulate assemblages, we performed linear regression analyses for each individual tooth specimen,
212 comprising four major ungulate families (Equidae, Rhinocerotidae, Cervidae and Bovidae), as well
213 as for average $\delta^{13}\text{C}$ and mesowear values in the four major localities studied here.
214 We used both parametric and nonparametric tests with $\alpha=0.05$ level of significance. Since ANOVA
215 is robust enough to handle departures from normality and unequal variances, and the distribution in
216 our samples did not significantly depart from normal to affect t-test statistics, we incorporated it to
217 see the differences in means among the sites. To identify the sources of significant differences in
218 these multiple comparisons, we used post hoc Tukey tests. We also confirmed all results using non-
219 parametric tests of Mann-Whitney and Kruskal-Wallis among species because they make no
220 assumptions about the sample distributions (normality).

221 **3. Results**

222 **3.1 Mesowear and carbon stable isotopes**

223 The $\delta^{13}\text{C}$ values in the studied species varied from -17.2 ‰ to -10.4 ‰ (Tables 2, 3; Figure 3). The
224 range of variation in $\delta^{13}\text{C}$ was higher in the temperate localities compared to the boreal ones.

225 The correlation between mean mesowear values and mean $\delta^{13}\text{C}$ among the ungulate locality
226 assemblages was very strong, positive and statistically significant, even though only four localities
227 were compared ($R^2 = 0.99$, $p = 0.002$) (Figure 4a). The regression between the carbon isotopic and
228 mesowear values for the individual tooth specimens also showed a barely significant but weak
229 positive correlation ($R^2 = 0.11$, $p = 0.006$) (Figure 4b, 4c). The only family to show a more
230 significant correlation between mesowear values and carbon isotopic values was Rhinocerotidae (R^2
231 $= 0.33$, $p = 0.05$).

Both *Cervus elaphus* and *Stephanorhinus kirchbergensis* had mean mesowear values of 1 without variation. The mean $\delta^{13}\text{C}$ for *Cervus elaphus* was -14.0 ‰ with the offset (+14‰) of the mean ecosystem value of -28.0 ‰ with very high variation (Table 2), and for *Stephanorhinus kirchbergensis*, -13.1 ‰ and -27.1 ‰ with low variation.

Megaloceros giganteus, *Dama dama*, *Stephanorhinus hundsheimensis* and *S. hemitoechus* had relatively low mean mesowear values of 1.1 – 1.2 and low variation. The mean $\delta^{13}\text{C}$ values and the mean ecosystem values were respectively -13.8 ‰ and -27.8 ‰ for *Megaloceros giganteus* with great variability, -14.8 ‰ and -28.8 ‰ for *Dama dama*, -14.0 ‰ and -28.0 ‰ for *Stephanorhinus hundsheimensis*, and -14.0 ‰ and -28.0 ‰ for *S. hemitoechus*, both species with some variability.

The large bovids, *Bison priscus* and *Bos primigenius*, had intermediate mesowear values of 1.7 and 1.4, respectively. *Bison priscus* demonstrated higher and more variable mean mesowear value ($\sigma = 0.4$) than *Bos primigenius* ($\sigma = 0.2$). The mean $\delta^{13}\text{C}$ values and the mean ecosystem values for *Bison priscus* were, respectively, -11.3 ‰ and -25.3 ‰, and for *Bos primigenius* -11.4 ‰ and -25.4 ‰ with similar variation. (Table 2)

Equus ferus had very high mean mesowear value of 2.2 and highly variable values ($\sigma = 0.6$). The mean carbon isotopic values and the mean ecosystem values for *Equus ferus* were, respectively, -12.9 ‰ and -26.9 ‰. The other equid species, *E. mosbachensis* and *E. hydruntinus*, showed relatively high but much lower mean mesowear values than *E. ferus*. The mean $\delta^{13}\text{C}$ values and the mean ecosystem values for *E. mosbachensis* were -13.1 ‰ and -27.1 ‰, respectively. For *E. hydruntinus* $\delta^{13}\text{C}$ was -12.7 ‰ and ecosystem $\delta^{13}\text{C}$ values -26.7 ‰.

Finally, *Coelodonta antiquitatis* demonstrated an extremely abrasion-dominated mesowear value of 3. The mean tooth enamel $\delta^{13}\text{C}$ values and the mean ecosystem $\delta^{13}\text{C}$ values for *C. antiquitatis* were, respectively, -11.7 ‰ and -25.7 ‰. (Table 2).

3.2 Mesowear, oxygen stable isotopes and temperature

The $\delta^{18}\text{O}$ values in the studied species varied from -10.9 ‰ to -2.1 ‰ (VPDB), from 19.6 ‰ to 28.7 ‰ (CO_3 VSMOW) (Tables 2, 3; Figure 3), 10.9 ‰ and 19.7 ‰ (PO_4 VSMOW), indicating that water sources used had the $\delta^{18}\text{O}_{\text{water}}$ values between -15.2 ‰ and -5.2 ‰, and extrapolated temperature -1.4 °C and 16.6 °C. The most variability in $\delta^{18}\text{O}$ and temperature was demonstrated by *Megaloceros giganteus*, *Cervus elaphus*, *Bos primigenius*, *Equus ferus* and *Equus mosbachensis* (Table 2).

The regression between extrapolated temperature and mesowear values for the individual tooth specimens showed a statistically significant but weak negative correlation ($R^2 = 0.19$, $p < 0.002$) (Figure 5a, b). The only family to show significant correlation between mesowear values and $\delta^{18}\text{O}$ values and temperature was Rhinocerotidae ($\delta^{18}\text{O}$ $R^2 = 0.64$, $p = 0.02$; temperature $R^2 = 0.5$, $p = 0.01$).

The range of variation in oxygen isotopic abundances and temperature was higher in the two temperate site assemblages compared to the two open and cold or boreal site assemblages.

The average temperature in localities based on the studied ungulates appeared to be 5.7°C in Mauer, 7.6°C in Steinheim combined, 3.6°C in Steinheim Sammet, 3.8°C in Villa Seckendorff (Table 4, Figure 6 a, b), although there was a lot of overlapping.

Significant variation occurred between the species of the two open and two closed site assemblages (ANOVA $F_{1, 65} = 26.15$, $p < 0.001$), oxygen VSMOW (ANOVA $F_{1, 65} = 4.09$, $p = 0.047$), oxygen VPDB (ANOVA $F_{1, 65} = 4.03$, $p = 0.049$), temperature (ANOVA $F_{1, 65} = 17.69$, $p < 0.001$), mesowear (ANOVA $F_{1, 65} = 8.31$, $p = 0.005$).

Within localities, in Villa Seckendorff we obtained the coldest temperature values in *Bos primigenius*, and the warmest in *Cervus elaphus* the warmest, in Steinheim Sammet *Equus ferus* the coldest and *Bos primigenius* the warmest, in Mauer *Equus mosbachensis* the coldest and

279 *Stephanorhinus etruscus* the warmest, in Steinheim combined *Cervus elaphus* the coldest and
280 *Megaloceros giganteus* the warmest.

281 **4. Discussion**

282 **4.1 Relationship between mesowear and $\delta^{13}\text{C}$**

283 A strong positive correlation between the mean $\delta^{13}\text{C}$ (proxy for habitat openness) and mean
284 mesowear (proxy for diet abrasiveness) at the level of localities or fossil assemblages demonstrates
285 a robust relationship between them, since the localities represent a more consistent combination of
286 ecological features. This indicates that the averaged feeding signal of a temperate or boreal ungulate
287 assemblage reflects habitat openness, despite there being differences in feeding ecology among the
288 ungulates, constituting these assemblages. A positive correlation between mesowear and $\delta^{13}\text{C}$
289 abundance probably reflects a tendency of ungulates to consume more abrasive plant material, such
290 as grasses and sedges, present more in open environments compared to closed ones (Saarinen et al.,
291 2016; Saarinen and Lister, 2016).

292 In tropical environments this pattern is more straightforward. Louys et al. (2012) compared stable
293 carbon isotopes and mesowear signals from tooth enamel of African antelopes and showed that they
294 were significantly correlated. In tropical and subtropical Africa, the carbon isotope composition in
295 tooth enamel reflects the proportion of C4 photosynthesizing plants, which are mostly grasses
296 (Cerling, 1992; Louys et al., 2012), in the animals' diet, and that is why a relatively strong
297 correlation between mesowear and $\delta^{13}\text{C}$ values would be expected, since both mesowear and $\delta^{13}\text{C}$
298 are considered to be proxies for grazing in this case.

299 However, this pattern does not appear to be universal and appears elusive at the individual species
300 level because feeding ecology and dietary specializations vary considerably within herbivores. In
301 the case of mid latitude Pleistocene ungulate assemblage, the $\delta^{13}\text{C}$ values do not indicate how much

302 of the animals' diet consisted of abrasive material, such as grass, because all studied species
303 indicate a pure C3 plant diet, but instead it is a proxy for vegetation openness. Different feeding
304 ecology, high variation in $\delta^{13}\text{C}$ compared to mesowear among individual species, and the fact that
305 the variations in $\delta^{13}\text{C}$ values in mid and high latitudes reflect habitat openness and the canopy effect
306 rather than differences in plant communities between the amount of grasses and browses available,
307 likely explain, why the correlation between stable carbon isotope values and mesowear values is
308 weak at the individual level.

309 Nevertheless, a positive correlation in this case is to be expected, because abrasive plants, such as
310 grasses and sedges, tend to be abundant in open environments. The most probable explanation for
311 this pattern is that both average dietary signals of local ungulate faunas (including interspecific as
312 well as intraspecific variables) reflect habitat openness in a very similar manner.

313 The sample sizes in our study are in most cases much too low for comprehensive conclusions about
314 the mean, and especially about the variations in the intraspecific mesowear and $\delta^{13}\text{C}$ values.

315 Nevertheless, the results show patterns, which are highly consistent with what is known or
316 suggested about the diets of the studied species (Geist, 2000; Gebert and Verheyden-Tixier, 2001;
317 Van Vuure, 2005; Rivals et al., 2007; Hall, 2008; Rivals et al., 2009; Hernesniemi et al., 2011;
318 Kahlke and Kaiser, 2011).

319 Mesowear values indicate that the red deer *Cervus elaphus* and the Merck's rhinoceros
320 *Stephanorhinus kirchbergensis* were browsers in the localities studied here. $\delta^{13}\text{C}$ values suggest a
321 rather forested landscape for both species with slight variations towards the open habitat on the
322 edge of the shrubland. *Cervus elaphus* demonstrated high habitat variability from grassland to dense
323 forests, consistent with isotopic data from bone collagen in Pleistocene and Holocene sites (e.g.
324 Drucker et al., 2011; Bocherens, 2014). *Stephanorhinus kirchbergensis* has been known as the
325 forest representative since its appearance in the temperate environments of Eurasia along with the

326 narrow-nosed rhinoceros *S. hemitoechus*, both substituting *Stephanorhinus hundsheimensis*
 327 (Beljaeva and David, 1975; Pushkina, 2007). Curiously, *S. hundsheimensis* $\delta^{13}\text{C}$ values appeared in
 328 between the values of both successive rhinoceroses, suggesting diet or habitat partitioning among
 329 these species.

330 A slightly variable mesowear of *Megaloceros giganteus*, *Dama dama*, *Stephanorhinus*
 331 *hundsheimensis* and *S. hemitoechus* indicates that they were mixed feeders, and $\delta^{13}\text{C}$ values indicate
 332 forested landscape for these species, except for one *S. cf. hemitoechus* value higher than the rest,
 333 suggesting an animal dwelling in the shrubland. As it has been already reflected in Pushkina et al.
 334 (2014), the narrow-nosed rhinoceros appeared to have favoured relatively forested environments
 335 along with the Merck's rhino *Stephanorhinus kirchbergensis*, even though it has been proposed to
 336 be a grazer from steppe environments, based on skull morphology (Loose, 1975; Pushkina, 2007).

337 The Giant deer *Megaloceros giganteus* is indicated to have been a forest species as soon as the type
 338 of habitat becomes available, however, apparently closer to the edge, and not in as dense forest as
 339 the smaller deer with smaller and simpler antlers, which is in an agreement with previous studies
 340 (Stuart et al., 2004). Very low $\delta^{13}\text{C}$ values in the giant deer can also be associated with its feeding in
 341 the forest understorey along with the red deer. During the glacial periods the giant deer appears to
 342 have persisted in the grasslands or Eurasian steppe (Pushkina et al., 2014).

343 Mesowear values of *Bison priscus* and *Bos primigenius* indicate that they were mixed feeders with
 344 *B. priscus* having had more abrasion-dominated and probably more variable diet. $\delta^{13}\text{C}$ results
 345 support the mesowear implications, suggesting grassland open environments for both species.
 346 Bovids exhibited the highest $\delta^{13}\text{C}$ values, indicating the most open steppe-tundra environments. The
 347 adaptation and specialization to the most open landscapes occurred already at the earlier
 348 evolutionary stage during the Saalian, which is already indicated in bovids from Steinheim Sammet

349 by highest $\delta^{13}\text{C}$ values, despite the presence of other types of more closed habitat (Pushkina et al.,
350 2014).

351 Mesowear values for *Equus ferus* indicate that it was a flexible grass-dominated feeder. This result
352 is based on a relatively large sample size. $\delta^{13}\text{C}$ results suggest semi-opened shrubland and woodland
353 habitat for *E. ferus*, which is also consistent with previous studies on the late Middle and Late
354 Pleistocene horses from German sites (Steinheim an der Murr) (van Asperen, 2010; Pushkina et al.,
355 2014).

356 The $\delta^{13}\text{C}$ for *E. mosbachensis* and *E. hydruntinus* indicate that they inhabited shrubland and
357 woodland. *E. mosbachensis* appeared more as a woodland edge horse, which is consistent with the
358 study of Kuitens et al. (2015) on $\delta^{13}\text{C}$ from collagen from *E. mosbachensis* in Schöningen that
359 suggested values for the light forest habitat. The sample size of the Pleistocene ass is not enough for
360 definite conclusions based on a single specimen of *E. hydruntinus* but still indicate their rather open
361 habitats. Steinheim *E. hydruntinus* occupied an ecological niche between bovids in extremely open
362 habitat and horses in shrubland – woodland (Pushkina et al., 2014). Based on the Holocene
363 zooarchaeological spatial and temporal latest occurrence data, highly fragmented *Equus*
364 *hydruntinus* populations were associated with separate regions of open habitat (Cres and Turvey,
365 2014).

366 The woolly rhinoceros *C. antiquitatis* appears to be a specialized grazer based on the highest
367 mesowear signal from the only two specimens, indicating abrasion-dominated diets, and open
368 grassland habitats. This is consistent with *C. antiquitatis* having inhabited cold open steppe or
369 tundra in south-western Germany by the late Weichselian and become adapted to the cold and arid
370 habitats (Pushkina et. al., 2014).

371 The strong positive correlation between mesowear and $\delta^{13}\text{C}$ as well as strong negative correlation
372 between mesowear and $\delta^{18}\text{O}$ in Rhinocerotidae occurs because the family is represented by the
373 species quite diverse in their ecology and diet. The woolly rhinoceros with the highest mesowear
374 value of blunter teeth represents cold and open habitats, and *Stephanorhinus* genus, all of which in
375 our study have rather low mesowear values of somewhat sharper teeth, indicating more browse-
376 dominated diets and warmer and woodland or forested habitats.

377 **4.2 Ecosystems based on $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$**

378 The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values demonstrated that the species in mid latitudes in south-western Germany
379 exploited the habitats from arctic tundra to rather dense forests. The same species demonstrated
380 considerable individual variation in ingested water source in different spatiotemporal
381 circumstances, depending on, whether it is found in glacial or temperate locality, suggesting they
382 were obtaining water resources from different in humidity and elevation sources. The largest
383 variation in water source and temperature occurred in large cervids, horses, aurochs and rhinos, all
384 of which were associated with forest or woodland environments, where the canopy effect, due to
385 variations in relative humidity and evapotranspiration on $\delta^{18}\text{O}$, must have been more profound than
386 in the open steppe environment. The differences in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ suggests niche partitioning and
387 interspecific competition between the species exploiting similar habitat, especially from the same
388 Family, as well as niche partitioning during the glacial and interglacial periods.

389 The large ungulates in south-western Germany showed less variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ during the
390 glacial periods or in the cold and open boreal environments, which is probably related to species
391 ecological flexibility and the breadth of choice among available ecosystems. A decreased variability
392 in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ composition can also be interpreted as the loss of ecological flexibility during the
393 glacial periods and increased ecologically flexibility at the species “dawn” or origination during

earlier evolutionary stages (Pushkina et al., 2014). Apparently, the availability and variety of ecosystems during glacial periods was decreased as well as it is at present in colder areas.

Remarkably, despite the fact that $\delta^{18}\text{O}$ values are difficult to interpret, especially in mid-latitudes, where the ingested water can be obtained from various sources, it appears from our study that ungulates with more abrasion-dominated mesowear signals in several south-western German sites demonstrated more enriched $\delta^{13}\text{C}$ values and less enriched $\delta^{18}\text{O}$ and lower temperature or association with more open and cold landscapes than ungulates with sharper teeth, which demonstrated lower carbon isotope abundances and higher temperatures or more forested, humid and warmer landscapes.

Conclusions

In the case of mid-latitude Pleistocene ungulate assemblages, analysed here, the correlation between $\delta^{13}\text{C}$ and mesowear is not straightforward because of a considerable variation in dietary specializations within herbivorous mammals. The $\delta^{13}\text{C}$ values do not indicate how much of the animals' diet consisted of abrasive material such as grass, but instead it is a proxy for overall vegetation openness. Nevertheless, a positive correlation in this case is demonstrated because abrasive plants, such as grasses and sedges, tend to be more abundant in open than in closed forested environments. As a summary, the families Cervidae (*Cervus*, *Dama* and *Megaloceros*) and Rhinocerotidae (essentially *Stephanorhinus* genus, except *Coelodonta antiquitatis*) had on average relatively low and low-variation intraspecific mesowear values, which indicated mostly browse-dominated diets. Based on $\delta^{13}\text{C}$ these families, except for the woolly rhinoceros, inhabited mostly dense forests to woodlands and shrublands. The family Bovidae showed intermediate mesowear values indicating mixed-feeding diets and quite high $\delta^{13}\text{C}$ values indicating invariably most open habitats from tundra to grasslands or Eurasian steppe-tundra. The family Equidae and the specialized grazing rhinoceros *Coelodonta antiquitatis* had high and relatively variable in case of

418 horses mesowear values, indicating grass-dominated diets, whereas their $\delta^{13}\text{C}$ values indicating
419 semi-closed shrubland for horses and open grasslands for the woolly rhinoceros.
420 The correlation between mesowear and $\delta^{18}\text{O}$ is not straightforward because the latter can be
421 affected by numerous factors. However, there is an indication that in the Pleistocene mid-latitudes
422 abrasive plants tend to be found in colder, probably more continental environments, rather than
423 humid and warmer ones. The greatest temperature variation occurred in the species inhabiting or
424 foraging in the forest environment, where the canopy effect of the understorey probably came into
425 play.

426 We conclude that combining dental ecometrics with stable isotope biochemistry on a more
427 differentiated level in common species, present in several localities, can give an insight and indicate
428 the tendencies in fossil species paleoecology even in small datasets.

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- 638
639

640 Table 1. The species lists of the localities.

641

642 Table 2. The means of $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, mesowear and temperature with standard deviations (σ) and

643 sample sizes of the species.

644 Table 3. Stable isotopes ($\delta^{13}\text{C}$; $\delta^{18}\text{O}$) and mesowear of the individual species.

645

646 Table 4. Ecosystem representation of the sites (temperature calculated via formulas presented above,

647 after Lecuyer et al., 2010 and Skrzypek et al., 2011)

648 Figure 1. Regional setting.

649 Figure 2. Mesowear scoring (Fortelius and Solounias 2000) illustrated as outline drawings showing

650 the buccal view of herbivorous mammal's upper molars. A-E: ruminants and equids, F-G:

651 rhinoceroses. A) high relief ($a/b \geq 0.1$) and sharp cusps. B) high relief ($a/b \geq 0.1$) and rounded

652 cusps. C) low relief ($a/b < 0.1$) and sharp cusps. D) low relief ($a/b < 0.1$) and rounded cusps. E) low

653 relief ($a/b < 0.1$) and blunt cusps. F) high relief ($a/b \geq 0.03$) and sharp cusps. G) high relief ($a/b \geq$

654 0.03) and rounded cusps. H) low relief ($a/b < 0.03$) and blunt cusps. The examples are drawn after

655 actual specimens (A-B: *Megaloceros giganteus*, C: *Equus altidens*, D-E: *Equus ferus*, F:

656 *Stephanorhinus kirchbergensis*, G: *Stephanorhinus hemitoechus*, H: *Coelodonta antiquitatis*), and

657 are not to the same scale.

658 Figure 3. Stable carbon and oxygen isotope abundances in species

659 Figure 4 a, b, c. Regression between $\delta^{13}\text{C}$ and mesowear in site assemblages and in families.

660 Figure 5 a, b. Temperature and mesowear regression.

661 Figure 6 a, b. Ecosystem and temperature based on individual species in the sites (6a), in the species

662 (6b).

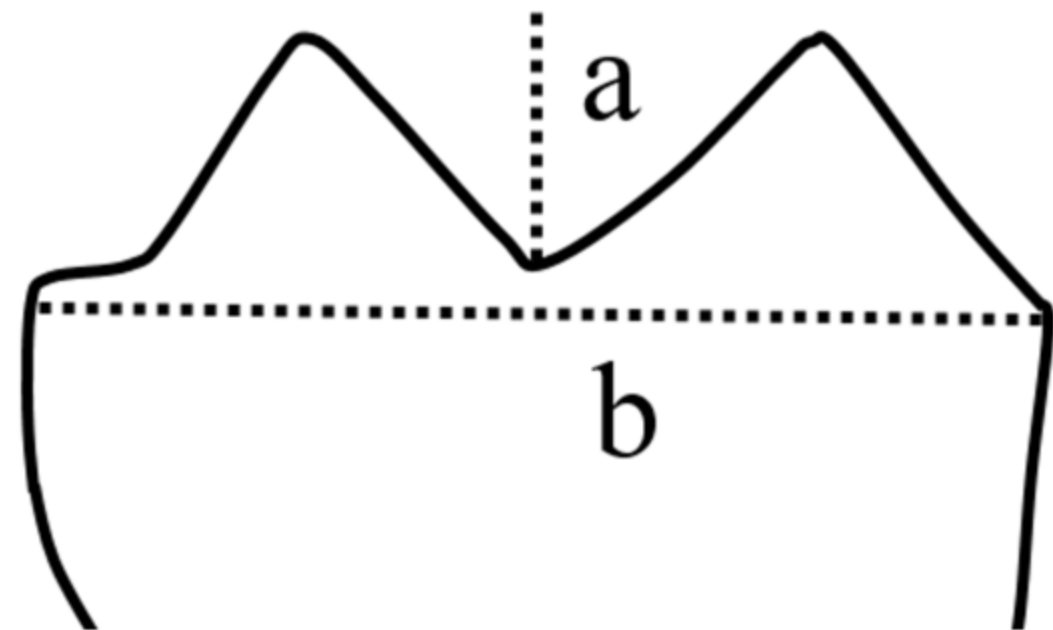


• Mauer
• Villa Seckendorf
• Steinhelm am der Murr

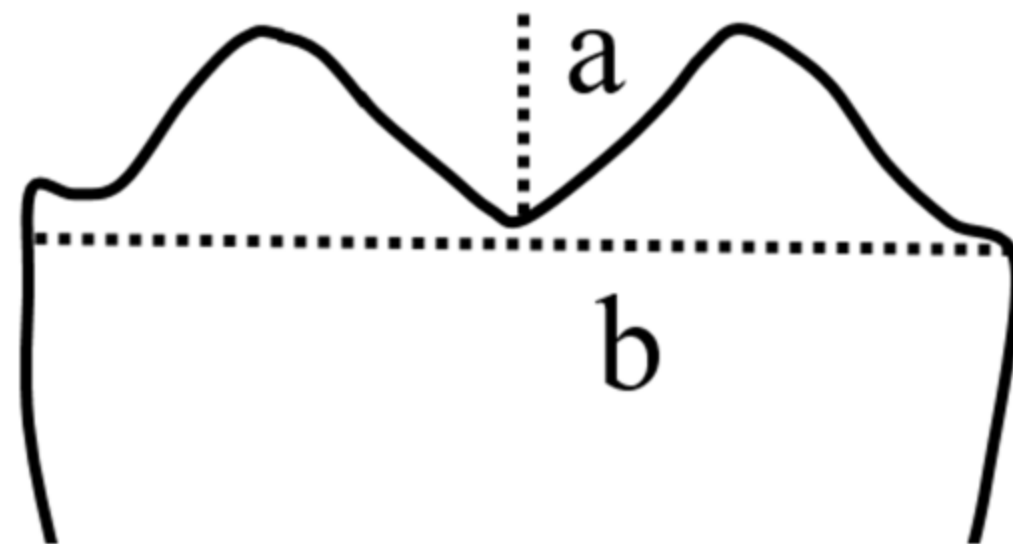
200 km

Ruminants and equids:

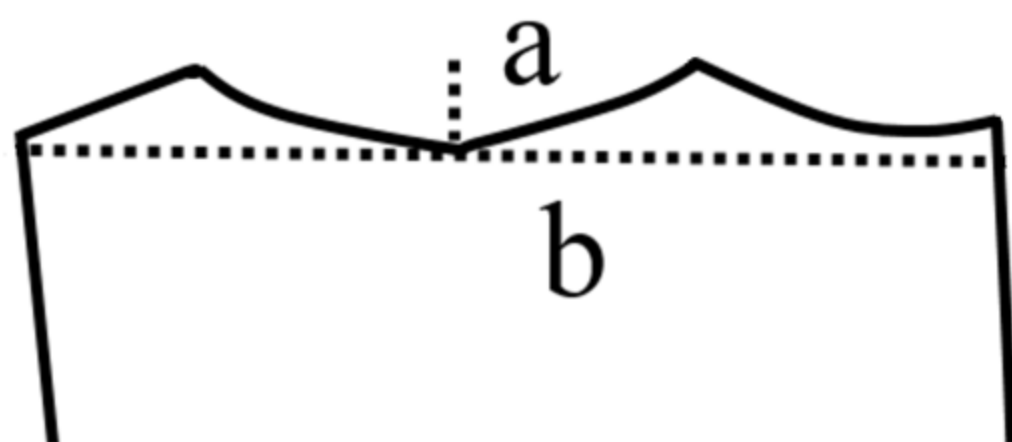
A



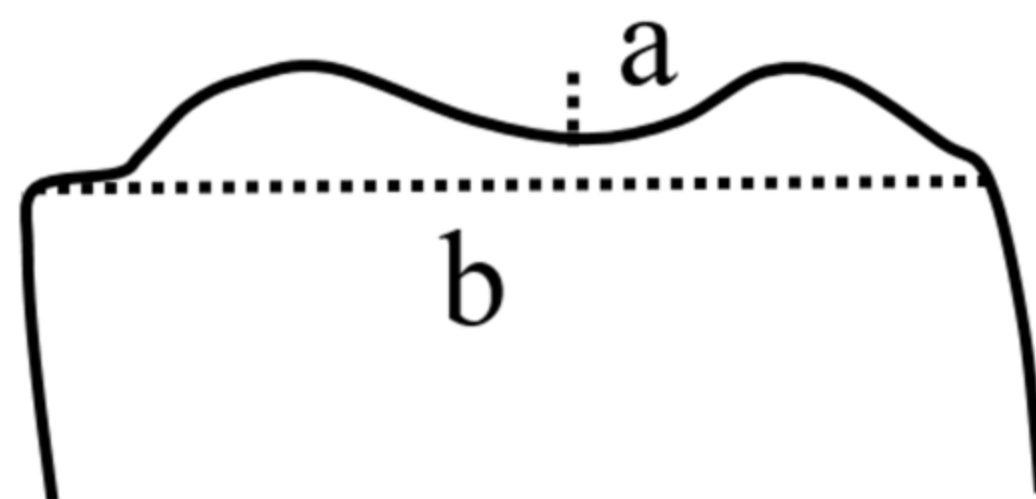
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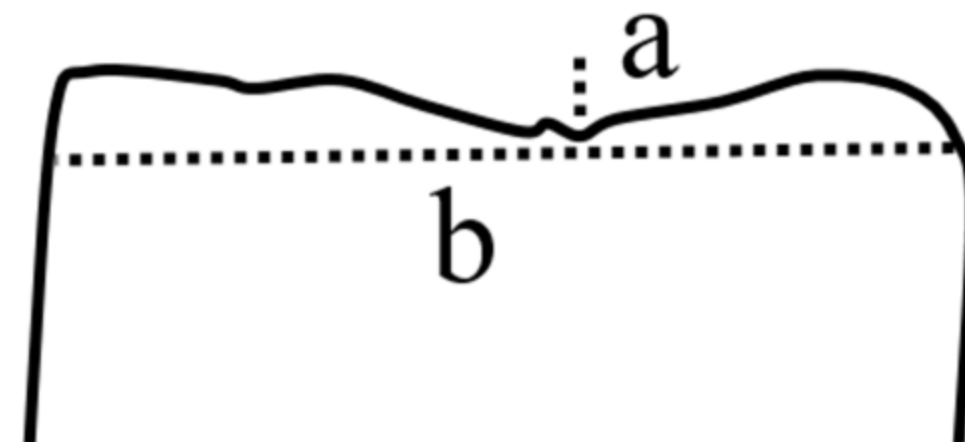
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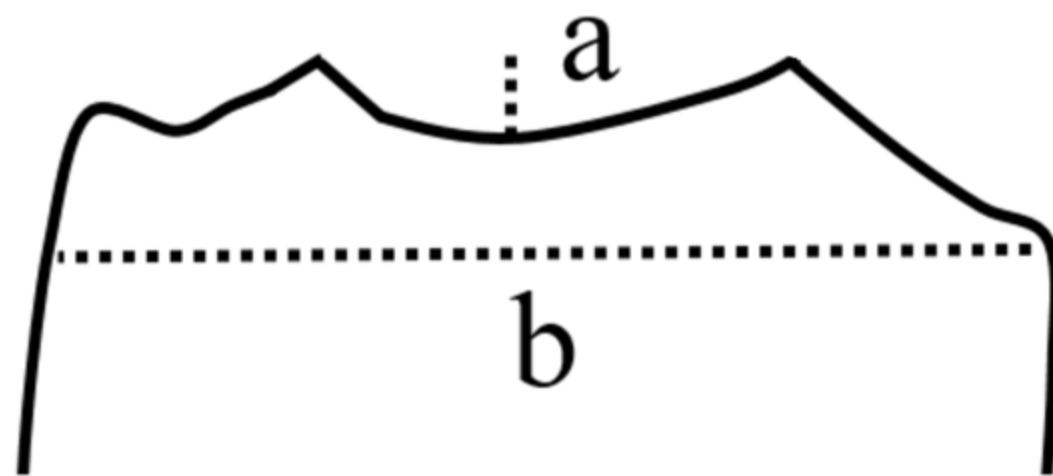


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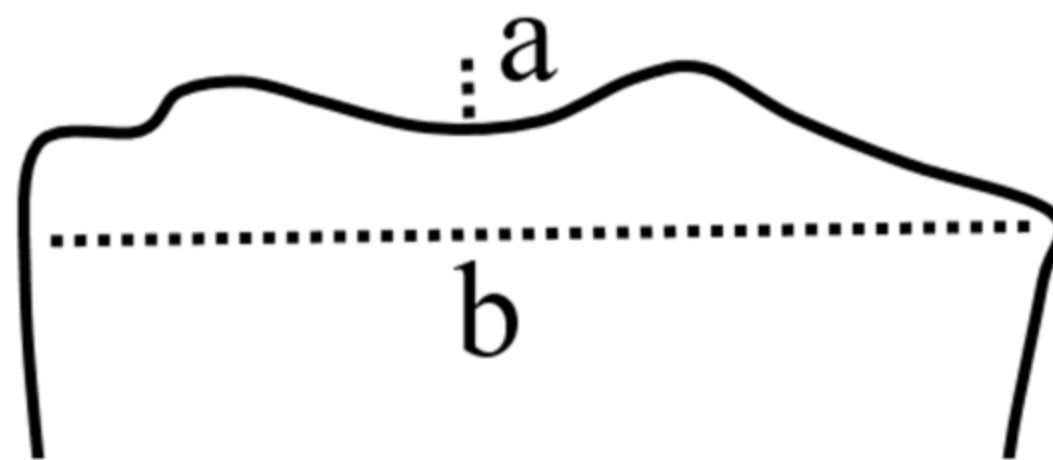


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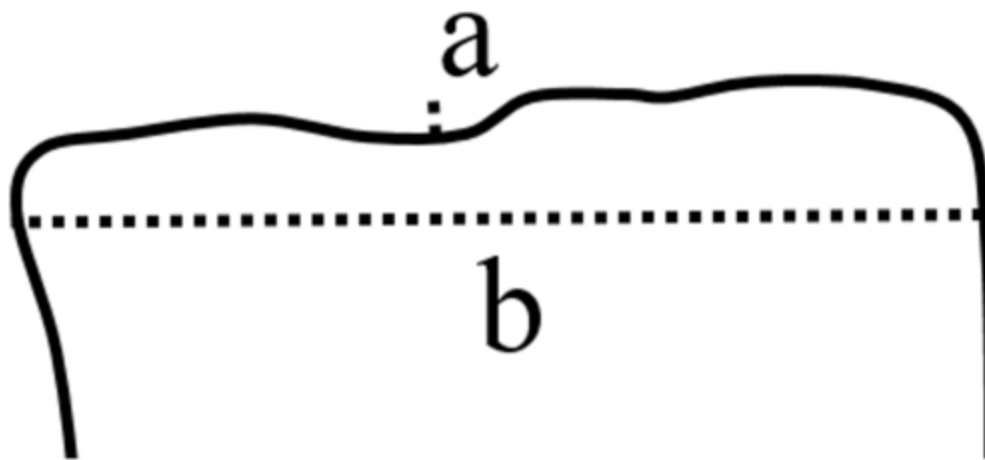
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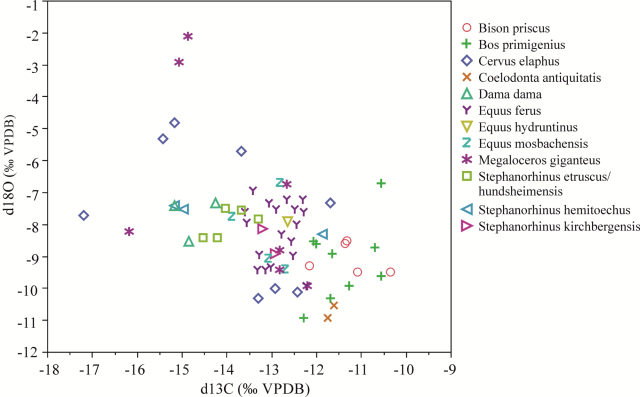


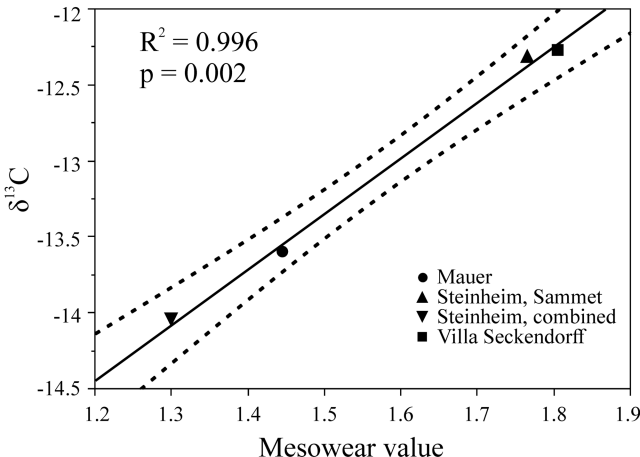
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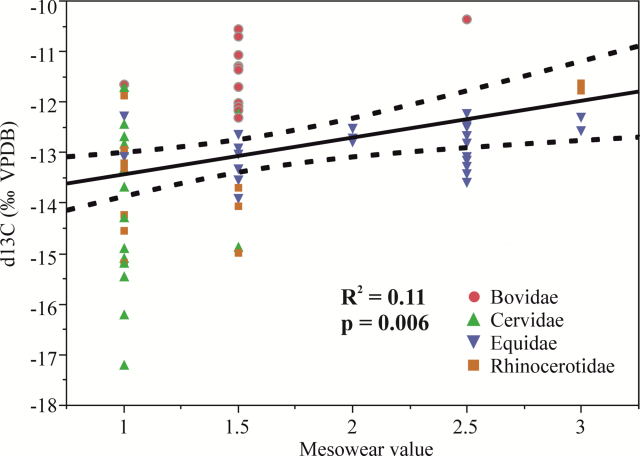


H









Generalized Linear Model Fit

Overdispersion parameter estimated by Maximum Likelihood

Response: $\delta^{13}\text{C}$ (‰ VPDB)

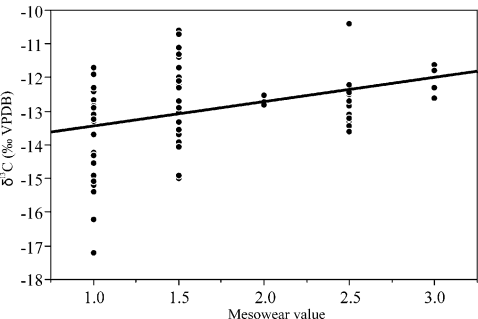
Distribution: Normal

Link: Identity

Estimation Method: Maximum Likelihood

Observations = 67

Regression Plot

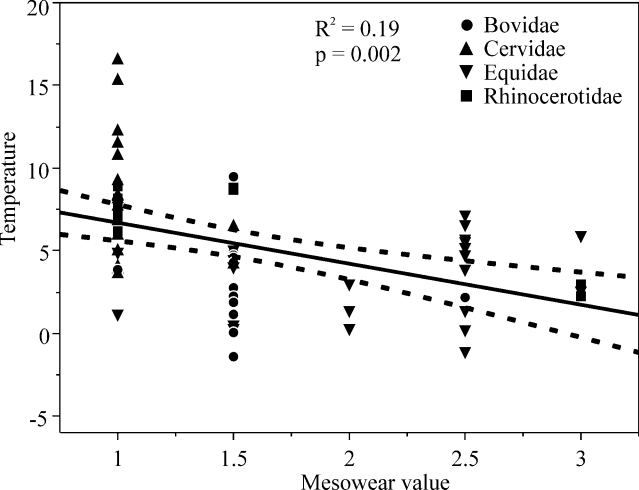


Likelihood-Ratio

Model	-LogLikelihood	ChiSquare	DF	P > ChiSq
Difference	3.96856811	7.9371	1	0.0048*
Full	112.133486			
Reduced	116.102054			

Goodness of

fit statistic	ChiSquare	DF	P > ChiSq	Overdispersion
Pearson	111.5066	65	0.0003*	1.6643
Deviance	111.5066	65	0.0003*	



Generalized Linear Model Fit

Overdispersion parameter estimated by Maximum Likelihood

Response: Temperature

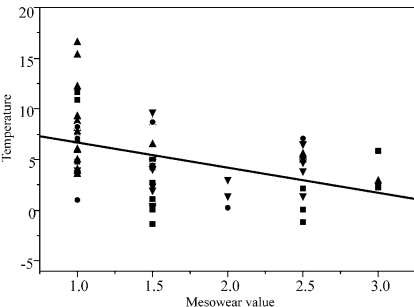
Distribution: Normal

Link: Identity

Estimation Method: Maximum Likelihood

Observations (or Sum Wgts) = 67

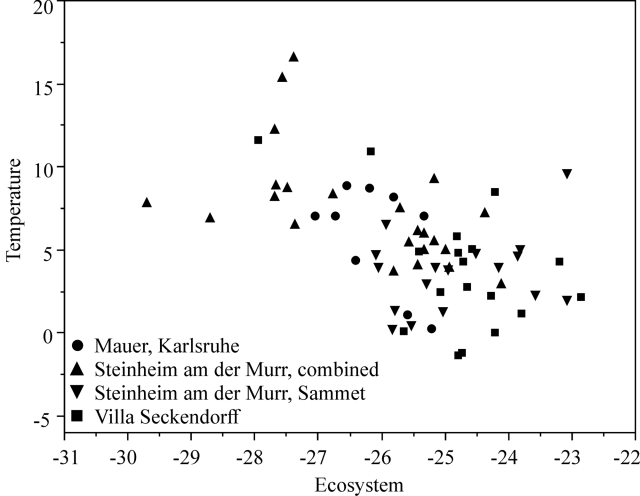
Regression Plot

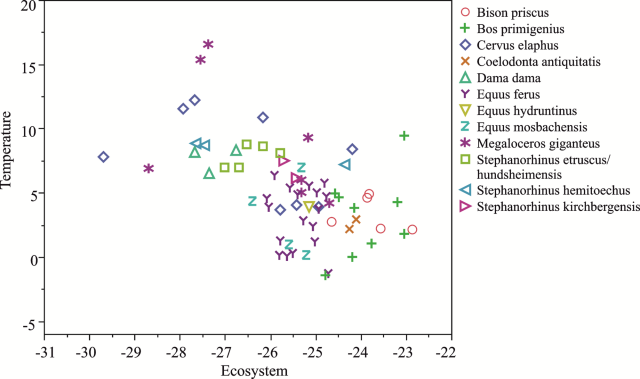


Model	-LogLikelihood	Likelihood-Ratio		
		ChiSquare	DF	P > ChiSq
Difference	7.02783836	14.0557	1	0.0002*
Full	173.977454			
Reduced	181.005292			

Goodness Of

Fit Statistic	ChiSquare	DF	P > ChiSq	Overdispersion
Pearson	706.3935	65	<0.0001*	10.5432
Deviance	706.3935	65	<0.0001*	





Locality	Chronostratigraphy	Species
Villa Seckendorff	late Weichselian MIS 5 a-d	<i>Bison priscus</i> <i>Bos primigenius</i> <i>Cervus elaphus</i> <i>Coelodonta antiquitatis</i> <i>Equus ferus</i> <i>Megaloceros giganteus</i>
Steinheim am der Murr, grube Sammet	Rissian (Saalian), MIS 10	<i>Bison priscus</i> <i>Bos primigenius</i> <i>Equus ferus</i> <i>Equus hydruntinus</i>
Steinheim an der Murr, combined from the pits (grube Sigris, Fritz, Bauer, Muller, Gruber)	Holsteinian, MIS 11	<i>Cervus elaphus</i> <i>Coelodonta antiquitatis</i> <i>Dama dama</i> <i>Equus ferus</i> <i>Megaloceros giganteus</i> <i>Stephanorhinus hemitoechus</i> <i>Stephanorhinus kirchbergensis</i>
Mauer	Cromerian, MIS 15	<i>Equus mosbachensis</i> <i>Stephanorhinus cf. hundsheimensis</i>

Family	Species	Sample size	Mean $\delta^{13}\text{C}$, ‰	Mean mesowear	Mean $\delta^{18}\text{O}$, ‰	Mean temperature
Cervidae	<i>Cervus elaphus</i>	8	-14.0 ± 1.8	1.0 ± 0.0	-7.7 ± 2.3	7.9 ± 3.6
Cervidae	<i>Megaloceros giganteus</i>	7	-13.8 ± 1.5	1.1 ± 0.2	-6.9 ± 3.2	9.1 ± 5.0
Cervidae	<i>Dama dama</i>	3	-14.8 ± 0.5	1.2 ± 0.3	-7.7 ± 0.7	7.8 ± 1.0
Bovidae	<i>Bos primigenius</i>	9	-11.4 ± 0.7	1.4 ± 0.2	-9.1 ± 1.2	3.3 ± 3.4
Bovidae	<i>Bison priscus</i>	5	-11.2 ± 0.7	1.7 ± 0.5	-9.1 ± 0.5	3.4 ± 1.3
Equidae	<i>Equus ferus</i>	18	-12.9 ± 0.5	2.2 ± 0.6	-8.2 ± 0.9	3.2 ± 2.4
Equidae	<i>Equus mosbachensis</i>	4	-13.1 ± 0.5	1.8 ± 0.7	-8.2 ± 1.3	3.2 ± 3.2
Equidae	<i>Equus hydruntinus</i>	1	-12.7	1.5	-7.9	3.9
Rhinocerotidae	<i>Stephanorhinus hundsheimensis</i>	5	-14.0 ± 0.5	1.2 ± 0.3	-7.9 ± 0.5	8.0 ± 0.9
Rhinocerotidae	<i>Stephanorhinus kirchbergensis</i>	2	-13.1 ± 0.2	1.0 ± 0.0	-8.5 ± 0.5	6.9 ± 1.0
Rhinocerotidae	<i>Stephanorhinus hemitoechus</i>	3	-14.0 ± 1.9	1.2 ± 0.3	-7.7 ± 0.5	8.3 ± 0.9
Rhinocerotidae	<i>Coelodonta antiquitatis</i>	2	-11.7 ± 0.1	3.0 ± 0.0	-10.7 ± 0.3	2.6 ± 0.6

Taxon	Site	d13Ccarb (‰ VPDB)	d 18O (‰ VPDB)	d 18O (‰ SMOW)	Ecosystem	Temperature	Mesowear
<i>Bison priscus</i>	Steinheim Sammet	-11.4	-8.6	22.0	-25.4	4.6	1.5
<i>Bison priscus</i>	Steinheim Sammet	-11.3	-8.5	22.1	-25.3	5.0	1.5
<i>Bison priscus</i>	Steinheim Sammet	-11.1	-9.5	21.1	-25.1	2.2	1.5
<i>Bison priscus</i>	Villa Seckendorff	-12.2	-9.3	21.3	-26.2	2.8	1.5
<i>Bison priscus</i>	Villa Seckendorff	-10.4	-9.5	21.0	-24.4	2.2	2.5
<i>Bos primigenius</i>	Steinheim Sammet	-12.0	-8.6	22.0	-26.0	4.8	1.5
<i>Bos primigenius</i>	Steinheim Sammet	-11.7	-8.9	21.7	-25.7	3.9	1
<i>Bos primigenius</i>	Steinheim Sammet	-10.6	-6.7	23.9	-24.6	9.5	1.5
<i>Bos primigenius</i>	Steinheim Sammet	-10.6	-9.6	20.9	-24.6	1.9	1.5
<i>Bos primigenius</i>	Villa Seckendorff	-12.3	-10.9	19.6	-26.3	-1.4	1.5
<i>Bos primigenius</i>	Villa Seckendorff	-12.1	-8.5	22.1	-26.1	5.0	1.5
<i>Bos primigenius</i>	Villa Seckendorff	-11.7	-10.3	20.2	-25.7	0.1	1.5
<i>Bos primigenius</i>	Villa Seckendorff	-11.3	-9.9	20.6	-25.3	1.1	1.5
<i>Bos primigenius</i>	Villa Seckendorff	-10.7	-8.7	21.9	-24.7	4.3	1.5
<i>Cervus elaphus</i>	Steinheim combined	-17.2	-7.7	23.0	-31.2	7.8	1
<i>Cervus elaphus</i>	Steinheim combined	-15.2	-4.8	25.9	-29.2	12.3	1
<i>Cervus elaphus</i>	Steinheim combined	-13.3	-10.3	20.3	-27.3	3.7	1
<i>Cervus elaphus</i>	Steinheim combined	-12.9	-10	20.5	-27.0	4.1	1
<i>Cervus elaphus</i>	Steinheim combined	-12.4	-10.1	20.5	-26.4	4.0	1
<i>Cervus elaphus</i>	Villa Seckendorff	-15.4	-5.3	25.4	-29.4	11.6	1
<i>Cervus elaphus</i>	Villa Seckendorff	-13.7	-5.7	25.0	-27.7	10.9	1
<i>Cervus elaphus</i>	Villa Seckendorff	-11.7	-7.3	23.4	-25.7	8.5	1
<i>Coelodonta antiquitatis</i>	Steinheim combined	-11.6	-10.5	20.0	-25.6	3.0	3
<i>Coelodonta antiquitatis</i>	Villa Seckendorff	-11.8	-10.9	19.6	-25.8	2.2	3
<i>Dama dama</i>	Steinheim combined	-15.2	-7.4	23.2	-29.2	8.2	1
<i>Dama dama</i>	Steinheim combined	-14.9	-8.5	22.1	-28.9	6.6	1.5
<i>Dama dama</i>	Steinheim combined	-14.3	-7.3	23.3	-28.3	8.4	1
<i>Equus ferus</i>	Steinheim Sammet	-13.6	-7.9	22.7	-27.6	3.9	1.5
<i>Equus ferus</i>	Steinheim Sammet	-13.4	-6.9	23.7	-27.4	6.5	2.5
<i>Equus ferus</i>	Steinheim Sammet	-13.3	-9.4	21.2	-27.3	0.2	1.5
<i>Equus ferus</i>	Steinheim Sammet	-13.3	-8.9	21.6	-27.3	1.3	2.5

<i>Equus ferus</i>	Steinheim Sammet	-13.0	-9.3	21.3	-27.0	0.4	1.5
<i>Equus ferus</i>	Steinheim Sammet	-12.8	-8.3	22.3	-26.8	2.9	2
<i>Equus ferus</i>	Steinheim Sammet	-12.5	-9.0	21.6	-26.5	1.3	2
<i>Equus ferus</i>	Steinheim Sammet	-12.5	-8.0	22.6	-26.5	3.8	2.5
<i>Equus ferus</i>	Villa Seckendorff	-13.2	-9.4	21.1	-27.7	0.1	2.5
<i>Equus ferus</i>	Villa Seckendorff	-12.9	-7.5	23.1	-26.9	4.9	1.5
<i>Equus ferus</i>	Villa Seckendorff	-12.6	-8.5	22.1	-26.6	2.5	3
<i>Equus ferus</i>	Villa Seckendorff	-12.3	-7.2	23.5	-26.3	5.9	3
<i>Equus ferus</i>	Villa Seckendorff	-12.3	-7.6	23.1	-26.3	4.8	1
<i>Equus ferus</i>	Villa Seckendorff	-12.2	-9.9	20.6	-26.2	-1.2	2.5
<i>Equus ferus</i>	Steinheim combined	-13.1	-7.3	23.3	-27.1	5.5	2.5
<i>Equus ferus</i>	Steinheim combined	-12.7	-7.2	23.4	-26.7	5.6	2.5
<i>Equus ferus</i>	Steinheim combined	-12.5	-7.5	23.2	-26.5	5.1	2.5
<i>Equus ferus</i>	Steinheim Sammet	-13.6	-7.6	23.0	-27.6	4.7	2.5
<i>Equus hydruntinus</i>	Steinheim Sammet	-12.7	-7.9	22.7	-26.7	3.9	1.5
<i>Equus mosbachensis</i>	Mauer. Karlsruhe	-13.9	-7.7	22.9	-27.9	4.4	1.5
<i>Equus mosbachensis</i>	Mauer. Karlsruhe	-13.1	-9.1	21.5	-27.1	1.1	1
<i>Equus mosbachensis</i>	Mauer. Karlsruhe	-12.8	-6.7	24.0	-26.8	7.1	2.5
<i>Equus mosbachensis</i>	Mauer. Karlsruhe	-12.7	-9.4	21.2	-26.7	0.2	2
<i>Megaloceros giganteus</i>	Steinheim combined	-16.2	-8.2	22.4	-30.2	7.0	1
<i>Megaloceros giganteus</i>	Steinheim combined	-15.1	-2.9	27.9	-29.1	15.4	1
<i>Megaloceros giganteus</i>	Steinheim combined	-14.9	-2.1	28.7	-28.9	16.6	1
<i>Megaloceros giganteus</i>	Steinheim combined	-12.8	-9.4	21.18	-26.8	5.1	1
<i>Megaloceros giganteus</i>	Steinheim combined	-12.8	-8.8	21.79	-26.8	6.0	1
<i>Megaloceros giganteus</i>	Steinheim combined	-12.7	-6.7	23.94	-26.7	9.4	1
<i>Megaloceros giganteus</i>	Villa Seckendorff	-12.2	-9.9	20.6	-26.2	4.3	1.5
<i>Stephanorhinus etruscus/hundsheimensis</i>	Mauer. Karlsruhe	-14.5	-8.4	22.2	-28.5	7.1	1
<i>Stephanorhinus etruscus/hundsheimensis</i>	Mauer. Karlsruhe	-14.2	-8.4	22.19	-28.2	7.1	1
<i>Stephanorhinus etruscus/hundsheimensis</i>	Mauer. Karlsruhe	-14.1	-7.5	23.16	-28.1	8.8	1.5
<i>Stephanorhinus etruscus/hundsheimensis</i>	Mauer. Karlsruhe	-13.7	-7.5	23.09	-27.7	8.7	1.5

<i>Stephanorhinus etruscus/hundsheimensis</i>	Mauer. Karlsruhe	-13.3	-7.8	22.8	-27.3	8.2	1
<i>Stephanorhinus hemitoechus</i>	Steinheim combined	-15.2	-7.4	23.2	-29.2	8.9	1
<i>Stephanorhinus hemitoechus</i>	Steinheim combined	-15.0	-7.5	23.1	-29.0	8.8	1.5
<i>Stephanorhinus hemitoechus</i>	Steinheim combined	-11.9	-8.3	22.3	-25.9	7.2	1
<i>Stephanorhinus kirchbergensis</i>	Steinheim combined	-13.2	-8.1	22.5	-27.2	7.6	1
<i>Stephanorhinus kirchbergensis</i>	Steinheim combined	-12.9	-8.9	21.7	-26.9	6.2	1

Site	Villa Seckendorff	Steinheim, Sammet	Steinheim, combined	Mauer
Ecosystem, ‰ Mean, SD (Min - Max)	forest, woodland, shrubland, grassland -26.3±1.1 (-29.4 - -24.4)	woodland, shrubland, grassland -26.3±1.0 (- 27.6 - -24.6)	dense forest, woodland, shrubland -27.8±1.5 (-31.2 - -25.6)	forest, woodland, shrubland -27.6±0.7 (-28.5 - -26.7)
Carbon, ‰ Mean, SD (Min - Max)	-12.3±1.1 (-15.4 - -10.4)	-12.3±1.0 (-13.6 - -10.6)	-13.8±1.5 (-17.2 - -11.6)	-13.6±0.6 (-14.5 - -12.7)
Oxygen, ‰ VPDB/ SMOW Mean, SD (Min - Max)	-8.7±1.6 (-10.9 - -5.3) 21.9±1.7 (19.6-25.4)	-8.5±0.9 (-9.6 - -6.7) 22.2±0.9 (20.9-23.9)	-7.7±2.1 (-10.5 - -2.1) 22.9±2.1 (20.0-28.7)	-8.1±0.8 (-9.4 - -6. 7) 22.6±0.9 (21.2-24.0)
Temperature, °C Mean, SD (Min - Max)	3.8±3.7°C (-1.4 – 11.6)	3.6±2.3°C (0.2 – 9.5)	7.6±3.4°C (3.0-16.6)	5.7± 3.2°C (0.2-8.8)